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A revision of the genus *Heterogorgia* Verrill, 1868 (Anthozoa: Octocorallia: Plexauridae)

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Abstract

The genus *Heterogorgia* Verrill, 1868 is poorly known. Lack of good illustrations and clear definitions have historically led authors to assign or transfer species erroneously to it. The genus was established by Verrill for three eastern Pacific species, another was described by Breedy and Guzman in 2005, and the geographic distribution was extended with the discovery of a western Atlantic species described by Castro in 1990. *Heterogorgia* is characterised by colonies composed of a number of stout stems that branch laterally and irregularly and arise from a conspicuous spreading holdfast. Coenenchymal sclerites are mostly colourless spindles; anthocodiae have strong spindles arranged in collaret and points; and the calyces are prominently armed with whorls of strongly projecting thorns. To define *Heterogorgia* we examined original type material of all eastern Pacific and western Atlantic species described until now and reference specimens from recent expeditions along the eastern Pacific. Morphological characters are analysed and illustrated using scanning electron micrographs. Lectotypes are designated for *H. tortuosa* and *H. verrucosa* to establish their taxonomic status. We conclude that *Heterogorgia* is comprised of five valid species at present: *Heterogorgia hickmani* and *H. verrucosa* for the Galapagos Islands and Ecuador mainland; *H. papillosa* for Mexico; *H. tortuosa* and *H. verrucosa* for Costa Rica and Panama; and *H. uatumani* for Brazil and Bahamas. The genera *Astromuricea*, *Bebryce*, *Echinogorgia* and *Psammogorgia* are proposed for the western Pacific species that were historically misplaced in *Heterogorgia*. We recommend that regional biodiversity estimates and biogeography analyses consider the erroneous status of the species that are still listed as *Heterogorgia* within the data sets.

Key words: Alcyonacea, Cnidaria, Coelenterata, eastern Pacific, gorgonians, soft corals, western Atlantic

Introduction

Heterogorgia was established by Verrill (1868) based on specimens collected in the tropical eastern Pacific; two species from Pearl Islands (Panama), *Heterogorgia verrucosa* and *Heterogorgia tortuosa*, and one species from La Paz (Mexico), *Heterogorgia papillosa.* After that, several old and new species from the western Pacific were either erroneously transferred or assigned to this genus by several authors, Thomson and Henderson (1905), Nutting (1910), and Kükenthal (1924). Later on, Harden (1979) reported the occurrence of the genus along the eastern Pacific and the coast of California, and Prahl *et al.* (1986) mentioned *H. verrucosa* in the Pacific of Colombia. More recently, two new valid species were added, *Heterogorgia uatumani* described by Castro (1990) from Ilha Grande (Brazil), and *Heterogorgia hickmani* described by Breedy and Guzman (2005) from Galápagos Islands (Ecuador).

The absence of good illustrations of the type species (*H. verrucosa*) and of holotype designations has made it difficult to characterise Verrill's genus and species (Castro 1990; Breedy & Guzman 2005). For this reason, Verrill's descriptions could fit several species. Thus, the need for a complete taxonomic revision has been historically recognised (Verrill 1912; Castro 1990; Bayer 1994; Breedy & Guzman 2005; Vargas *et al.* 2010). Herein, we revise the genus based on original type material of all the species from the eastern Pacific and Brazil, described to date and on reference specimens from recent surveys and expeditions along the tropical eastern Pacific. Due to the bad condition of the type material of two species, we designate lectotypes to clearly establish their identity. We also

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propose genera for the 14 errant species that have been included in *Heterogorgia* by many authors in the past. This research represents the fourth review in a series proposed to evaluate the genera of gorgonians reported for the shallow eastern Pacific waters. Previous reviews dealt with *Pacifigorgia* Bayer, 1951 (Breedy & Guzman 2002), *Leptogorgia* Milne Edwards & Haime, 1857 (Breedy & Guzman 2007) and *Eugorgia* Verrill, 1868 (Breedy *et al.* 2009), in the family Gorgoniidae.

Material and methods

Type material used in this study was analyzed during visits to, or borrowed from, the following institutions: California Academy of Science, Invertebrate Zoology, San Francisco, USA (CASIZ); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ); Museum of Natural History, Smithsonian Institution, Washington, USA (USNM); and Yale Peabody Museum of Natural History, New Haven, USA (YPM). In addition, specimens recently collected from along the Pacific coast of Mexico, Costa Rica, Panama, and Ecuador which are deposited, or kept as loans in the Museo de Zoología, Universidad de Costa Rica, Costa Rica (UCR), Smithsonian Tropical Research Institute, Panama (STRI), and Institute of Marine Research Nazca, Quito, Ecuador (IIN) were also studied. This material was mostly collected by scuba diving, down to 40 m in depth; some specimens were obtained by dredging to 60 m. For microscopic study, sclerites and axes were prepared for scanning electron microscopy (SEM) following the protocol described in Breedy and Guzman (2002) and photographed using a N-2360 Hitachi (at the Centro de Investigación en Estructuras Microscópicas, Universidad de Costa Rica, CIEMIC, UCR), and an MV 2300 CAM-SCAN (at Institut de Géologie et Paléontologie, Université de Lausanne). Measurements of the sclerites were obtained from pictures and directly from a light microscope using an optical micrometer. Length of the sclerites was measured from one tip to the other and the width was taken from the most distant points across the sclerites, recording the minimum and maximum dimensions found in the samples (which do not necessarily represent the largest sclerite in the illustrations because they break easily). Variation is expected in the diameter of stems and branches either in preserved or dry specimens, due to the preservation history of the specimens (Hickson 1928). Most of the type material is dry and old. Polyps from fresh material, when available, were dissected to examine anthocodial sclerite arrangements. The proposed genera for the misidentified *Heterogorgia* species is the result of type material examined (when it was available), literature, and expert's advice (S. Cairns, L. van Ofwegen) (Table 1).

Terminology used is based on or modified from Bayer *et al.* (1983), and Breedy & Guzman (2005).

Other Abbreviations.

CDRS Charles Darwin Research Station, Galápagos Islands, Ecuador; RMNH: Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands.

Class Anthozoa Ehrenberg, 1834

Subclass Octocorallia Haeckel, 1866

Order Alcyonacea Lamouroux, 1812

Family Plexauridae Gray, 1859

Heterogorgia Verrill, 1868

Heterogorgia Verrill, 1868: 413; Verrill 1869: 450 (emended); Studer 1887: 57; Wright & Studer 1889: 55; Nutting 1910: 87; Kükenthal 1919: 844; Kükenthal 1924: 229–230; Bayer 1956: F206; Harden 1979: 112; Bayer 1981: 931; Castro 1990: 412–415; Breedy & Guzman 2005: 801–803; Vargas *et al.* 2010: 4; Castro *et al.* 2010: 776.

Type species: *Heterogorgia verrucosa* Verrill, 1868, by subsequent designation (Nutting 1910: 87).

Diagnosis. (see also Verrill 1868; Castro 1990; Castro *et al.* 2010; Breedy & Guzman 2005).

The axis is horny, and colonies are composed of a number of stout stems that branch laterally and irregularly and arise from a conspicuous spreading holdfast. Coenenchyme is thin to moderately thick, mostly with a granulose surface. All sclerites are colourless. Coenenchymal sclerites are: radiates, strongly and unevenly tuberculated spindles, that may be branched, irregular spindle-derived forms, and crosses with the four arms of the same or different length. Polyps are retractile within protruding calyces; neck zone of the anthocodiae is without sclerites. Polyps are from bright yellow to colourless when alive and whitish when preserved in ethanol. Anthocodiae have a well defined collaret consisting of transverse rows of long, strong, bent spindles, and points consisting of long spiny spindles *en chevron*; some of the point spindles have a spiny tip which is in distal position. These sclerites vary in size and shape according to the species, but the same basic forms occur in each species. Calyces are prominent with a lobed rim that is armed with different numbers of whorls of strongly projecting thorns whose size and ornamentation is characteristic of each species. In carefully dried specimens the thorn arrangements of the calyx rim can be easily observed. According to Verrill (1868) the name *Heterogorgia* alludes to the remarkable diversity in the sizes and shapes of the sclerites.

The colour of the colonies is white, beige or greyish; when the colonies are dry or ethanol preserved, they acquire darker hues.

Remarks. About 14 species, excluding Verrill's species, have been assigned to this genus (Pallas 1766; Germanos 1896; Thomson & Henderson 1905; Thomson & Crane 1909; Nutting 1910; Kükenthal 1924), which present a wide morphological diversity, corroborating Verrill's (1912) statement that *Heterogorgia* was misunderstood by Nutting (1910) and some other authors. In reality, the genus probably became a "catch all" because it was not properly defined by Verrill himself, as mentioned above. The errant species, still recorded as belonging to *Heterogorgia,* fit in the genera, *Astromuricea* Germanos, 1896, *Bebryce* Philippi, 1841, *Echinogorgia* Kölliker, 1865, and *Psammogorgia* Verrill, 1868 (see Table 1). However; a thorough revision of these genera has to be made in order to identify the actual species with some certainty.

TABLE 1. Proposed genera for species misplaced in the genus *Heterogorgia* Verrill, 1868.

Species	Original author	Original genus	Author *	Proposed genus
H. clausa	Nutting, 1910	*Heterogorgia*		*Echinogorgia* Kölliker, 1865
H. flabellum	(Pallas, 1766)	*Antipathes* Pallas, 1766	Nutting 1910	*Psammogorgia* Verrill, 1868
H. gracilis	(Verrill, 1868)	*Psammogorgia* Verrill, 1868	Harden 1979	*Psammogorgia* Verrill, 1868
H. grandicalyx	Kükenthal, 1924	*Heterogorgia*		*Brebyce* Philippi, 1841
H. humilis	Nutting, 1910	*Heterogorgia*		*Echinogorgia* Kölliker, 1865
H. magna	Nutting, 1910	*Heterogorgia*		*Echinogorgia* Kölliker, 1865
H. muricelloides	Nutting, 1910	*Heterogorgia*		*Echinogorgia* Kölliker, 1865
H. operculata	Nutting, 1910	*Heterogorgia*		*Echinogorgia* Kölliker, 1865
H. polyklados	(Germanos, 1896)	*Astromuricea* Germanos, 1896	Kükenthal 1924	*Astromuricea* Germanos, 1896
H. ramosa	(Thomson & Henderson, 1905)	*Astromuricea* Germanos, 1896	Nutting 1910	*Echinogorgia* Kölliker, 1865
H. reticulata	Nutting, 1910	*Heterogorgia*		*Echinogorgia* Kölliker, 1865
H. stellata	Nutting, 1910	*Heterogorgia*		*Echinogorgia* Kölliker, 1865
H. stellifera	(Thomson & Crane, 1909)	*Astromuricea* Germanos, 1896	Kükenthal 1924	*Astromuricea* Germanos, 1896
H. theophilasi	(Germanos, 1896)	*Astromuricea* Germanos, 1896	Kükenthal 1924	*Astromuricea* Germanos, 1896
H. verrilli	Thomson & Henderson, 1905			? *Echinogorgia* Kölliker, 1865

(*) Author who transferred the original species to the genus *Heterogorgia*; (?) Uncertain genus.

***Heterogorgia hickmani* Breedy & Guzman, 2005**
(Figs. 1A–B, 2, 3)

Heterogorgia hickmani Breedy & Guzman, 2005: 803–806; Castro *et al.* 2010: 779.

FIGURE 1. Submarine photographs: (A–B) *H. hickmani*, Galápagos Islands, Ecuador (Photographs by H.P. Hickman); (C) *H. tortuosa*, Coiba Island, Panama; (D) *H. verrucosa*, Coiba Island.

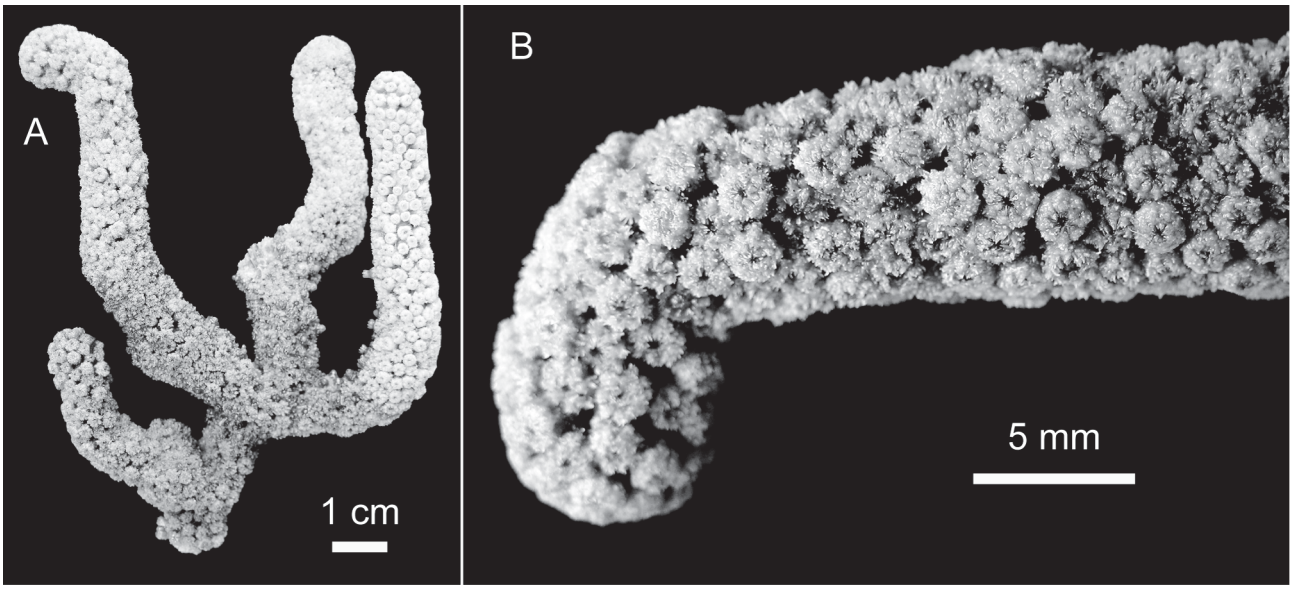

FIGURE 2. *Heterogorgia hickmani,* paratype, CDRS Ang. 156: (A) colony; (B) detail of a branch.

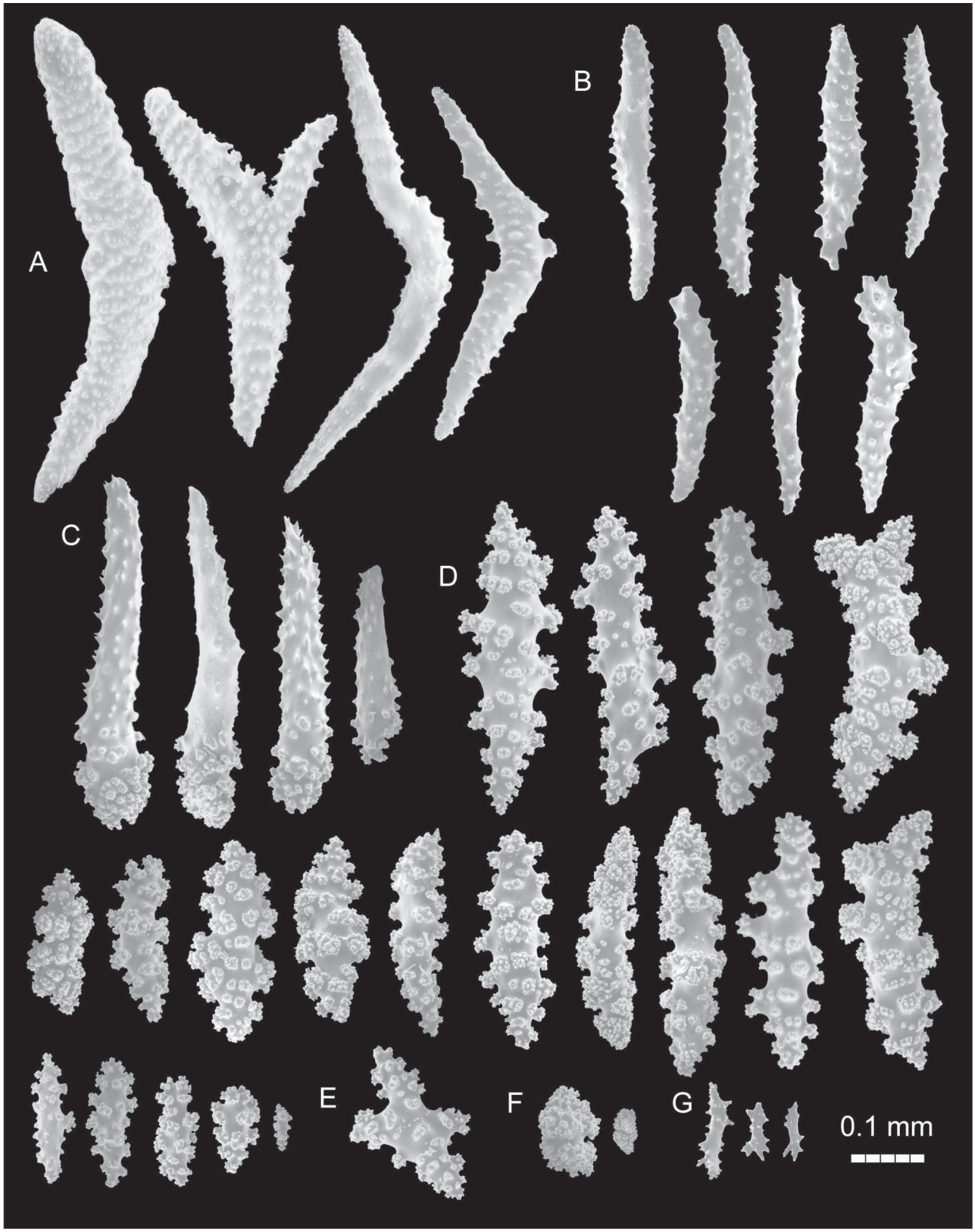

FIGURE 3. *Heterogorgia hickmani*, paratype, CDRS Ang. 156, sclerites: (A) collaret spindles; (B) point spindles; (C) thorns; (D) spindles; (E) cross; (F) irregular warty ovals; (G) tentacular rods.

Material examined. Holotype: CDRS 03–95, ethanol preserved, La Botella, Floreana Island, Galápagos Islands, 7.5 m, C. Hickman, 19 January 2003.

Paratypes: CDRS 03–699, ethanol preserved, Pinzón Island, Galápagos Islands, 7.5 m, C. Hickman, 18

November 2003; CDRS Ang 156, four fragments, ethanol preserved, La Botella, 6 m, A. Chiriboga, 25 May 2004; CDRS Ang 139, fragment, ethanol preserved, La Botella, 11 m, A. Chiriboga, 8 February 2004.

Other material. ECUADOR: IIN 50, 78, dry, Gigima, Reserva de Producción Faunística Marino Costera Puntilla de Santa Elena, 12–14 m, F. Rivera, P. Martínez, R. Nebot and O. Breedy, 22 July 2010; IIN 122, dry, Los Ahorcados Islet, Provincia de Manabí, F. Rivera, P. Martínez, R. Nebot and O. Breedy, 10–12 m, 25 July 2010; GALÁPAGOS ISLANDS: CDRS Ang. 122, ethanol preserved, Gordons Rock, 24 m, A. Chiriboga, 23 January 2004; CDRS 04-167, ethanol preserved, Los Cañones, Isabela, 11 m, A. Chiriboga, 9 October 2004; CDRS 04-317, ethanol preserved, Caleta Negra, 15 m, A. Chiriboga, 30 November 2004; CDRS CDRS 04-326, ethanol preserved, Las Marielas, 3 m, A. Chiriboga, 2 December 2004; CDRS 04-359, ethanol preserved, La Botella, 15 m, A. Chiriboga, 4 December 2004; CDRS 04-367, ethanol preserved, Kicker Rock, San Cristóbal, 15 m,A. Chiriboga, 5 December 2004; CDRS 04-370, ethanol preserved, Five fingers, San Cristóbal, 15 m, A. Chiriboga, 5 December 2004; CDRS 04-380, ethanol preserved, Santa Fe, 24 m, A. Chiriboga, 6 December 2004; CDRS 07-101-102, ethanol preserved, Don Ferdi, Brainbridge Rocks, 24–26 m, O. Breedy, 9 March 2007; CDRS 07-114, ethanol preserved, Gordons Rock, 24 m, O. Breedy, 10 March 2007; CDRS 07-124, ethanol preserved, San Cristóbal, 15 m, C.P. Hickman, 11 March 2007; CDRS 07-193, ethanol preserved, Pinzón, 15 m O. Breedy, 2 March 2007.

Description. Colonies are composed of a few thick stems, branched or unbranched and slightly crooked with a rounded tip (Figs. 1A, 2A), that are up to 18 cm long, and are connected at their base by a continuous encrusting holdfast. The diameter of branches including calyces is up to 15 mm, and about 19 mm at tips. When alive, the polyps are bright yellow and the coenenchyme looks brownish (Fig. 1A–B). The polyps are densely packed around the branches (40–50 calyces/cm), more scarcely distributed on the holdfast and at the base of branches. The calyces are prominent, up to 2 mm diameter with a spiny lobed rim, and up to 1 mm tall (Fig. 2A–B). The anthocodial armature consists of a strong collaret and points arrangement. The collaret is composed of three rows of long curved spindles 0.5–0.7 mm long and 0.05–0.13 mm wide, with small warts on their surface; some have one or two short branch-like projections at one side (Fig. 3A). The points consist of five pairs of warty spindles and rods, 0.35–0.50 mm long and 0.04–0.06 mm wide, arranged *en chevron* (Fig. 3B). The calicular rim has 3–4 whorls of long, strong, thorns, 0.3–0.5 mm long (Fig. 3C). The coenenchymal sclerites include spindles, straight, bent or irregularly branched, 0.25–0.45 mm long and 0.10–0.15 mm wide (Fig. 3D); irregular warty ovals, 0.06– 0.12 mm long and 0.04–0.07 mm wide (Fig. 3F); and crosses that are up to 0.10–0.25 mm (Fig. 3E). The tentacular thorny rods are 0.08–0.20 mm long and 0.02–0.05 mm wide (Fig. 3G). A more detailed description is given in Breedy & Guzman (2005).

The colour of the colonies is whitish to beige or greenish in ethanol or dry preserved.

Remarks. The stems with just one or two wide branches, the large calyces arranged very close together, and the predominance of larger sclerites distinguish this species from all others. This species has been found at several sites in the Galápagos Islands and recently off the mainland coast of Ecuador. There are no records elsewhere in the eastern Pacific.

Heterogorgia papillosa Verrill, 1870

(Figs. 4, 5)

Heterogorgia papillosa Verrill, 1870: 557; Kükenthal 1924: 232; Harden 1979: 113.

Material examined. Holotype: YPM 8609, dry, La Paz, Baja California Sur, Mexico, 11–15 m, J. Pedersen, date unknown.

Description of the holotype. The colony is 10.5 cm tall and 8 cm wide (Fig. 4A), consists of two main branches that arise from a naked, 1 cm long stem without holdfast. The branching is sparse and irregular; the branches subdivide up to four times, and are 3–4 mm in diameter. The calyces are prominent, about 0.5–1 mm tall and up to 0.5 mm diameter (Fig. 4A–B); they are distributed all around the branches, not very close together (20–25 calyces/cm); some are separated by up to 4 mm, and are even more distant at the base of branches. The anthocodial armature consists of collaret and points arrangements. The collaret is composed of one row of long, curved, acute spindles, 0.26–0.43 mm long and 0.03–0.05 mm wide (Fig. 5A); the points have two pair of spiny spindles arranged *en chevron*, 0.2–0.35 mm long and 0.02–0.04 mm wide (Fig. 5B). The calicular rim has two whorls of

thorns, 0.24–0.25 mm long and 0.04–0.06 mm wide, some of which are poorly developed and look like spindles (Fig. 5C). Tentacles have small, irregular rods 0.10–0.16 mm long and 0.015–0.02 mm wide (Fig. 4C). Coenenchymal sclerites include: small, tuberculate radiates, 0.07–0.09 mm long and 0.05–0.055 mm wide (Fig. 5E); spindles 0.15–0.4 mm long and 0.04–0.1 mm wide, including many different spindle-derived and branched forms with very irregular tuberculation (Fig. 5D); and crosses 0.08–0.14 mm diameter with tuberculate arms or tuberculate all over (Fig. 5F).

Colour of the colony is pale yellowish to white.

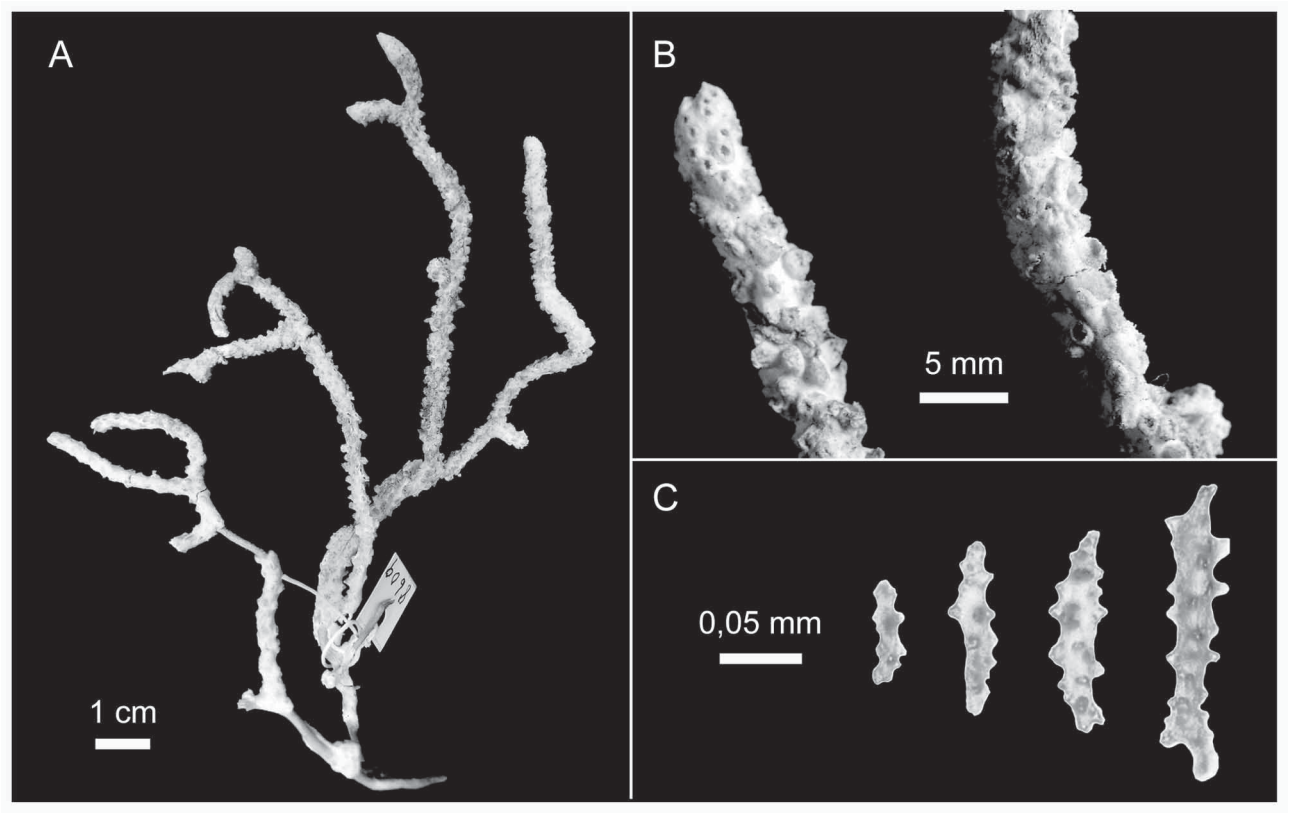

FIGURE 4. *Heterogorgia papillosa*, holotype, YPM 8609: (A) colony; (B) detail of a branch; (C) tentacular sclerites.

Remarks. The only known specimen of this species is the holotype. There is other material in the YPM from Mexico that includes specimens labelled as *H. papillosa*, but our examination has shown the species is not actually present. This species differs from the other three eastern Pacific species in its long, thinner branches and weaker collaret and points, and although it has similar colony form and collaret and points arrangement to *H. uatumani*, it differs in sclerite form and size (Table 2, Fig. 9).

This species is only known from the type locality.

Heterogorgia tortuosa Verrill, 1868

(Figs. 6, 7)

Heterogorgia tortuosa Verrill, 1868: 414; Verrill 1869: 452–454; Kükenthal 1924: 231; Harden 1979: 113–114.
Heterogorgia verrucosa Castro 1990: 412–415.

Material examined. Lectotype (here designated): YPM 1555d dry, Pearl Islands, Panama, depth not given, F. H. Bradley, 1866–1867.

Paralectotypes: BM 1950.31.62.45, YPM 1555a–c, MCZ 4910 dry, Pearl Islands, Panama, depth not given, F. H. Bradley, 1866–1867.

Other material. COSTA RICA: UCR 501, dry, Ana Bay, Caño Island, 17 m, H. Guzman, 10 February 1984; UCR 1854, preserved in ethanol, Nicoya Gulf, 11 m November 2002, O. Breedy; UCR 1865 (3), preserved in etha-

nol, Matapalo, Port Jiménez, 25 m, O. Breedy, 13 March 2004; UCR 1864 (2), preserved in ethanol, Ballena Marine National Park, 19 m, O. Breedy, 24 April 2002. PANAMA: UCR 1863 (2), preserved in ethanol, Jicarita southwest, Coiba Island, 21 m H. Guzman, April 2002; UCR 1858 (3), preserved in ethanol, Frailes south, 15 m, H. Guzman, December 2001; UCR 1862, preserved in ethanol, Bajo Viuda, Coiba Island, 18–20 m, H. Guzman, 22 April 2002; STRI 305, dry, Bajo La Viuda, 30 m, H. Guzman, 23 April 2002; SRTI 236, 237, dry, Islote, 10 m, H. Guzman, 20 April 2002; STRI 368, dry, Otoque Island, 5–10 m, H. Guzman, 9 May 2002.

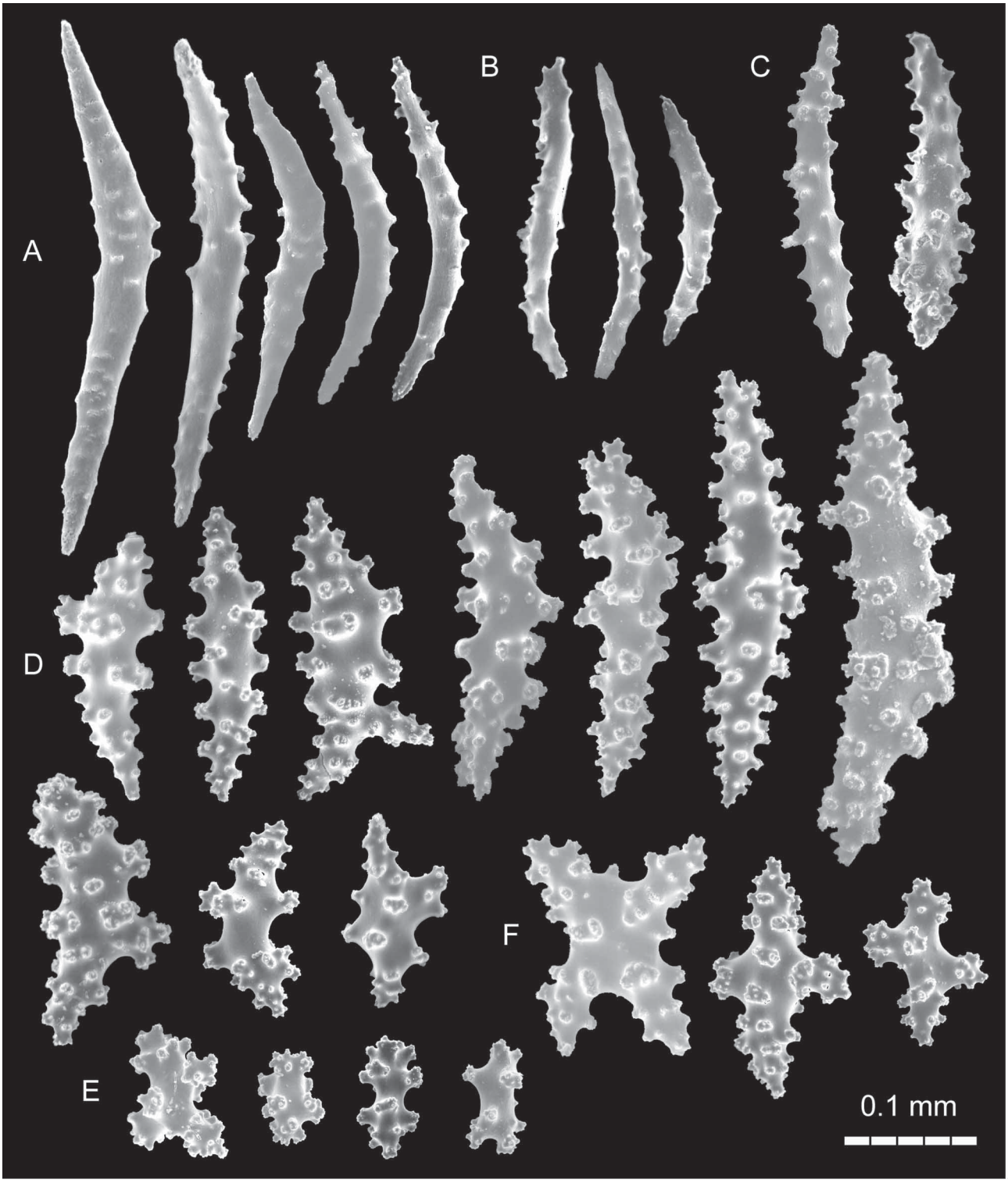

FIGURE 5. *Heterogorgia papillosa*, holotype, YPM 8609, sclerites: (A) collaret spindles; (B) point spindles; (C) thorns; (D) spindles; (E) radiates; (F) crosses.

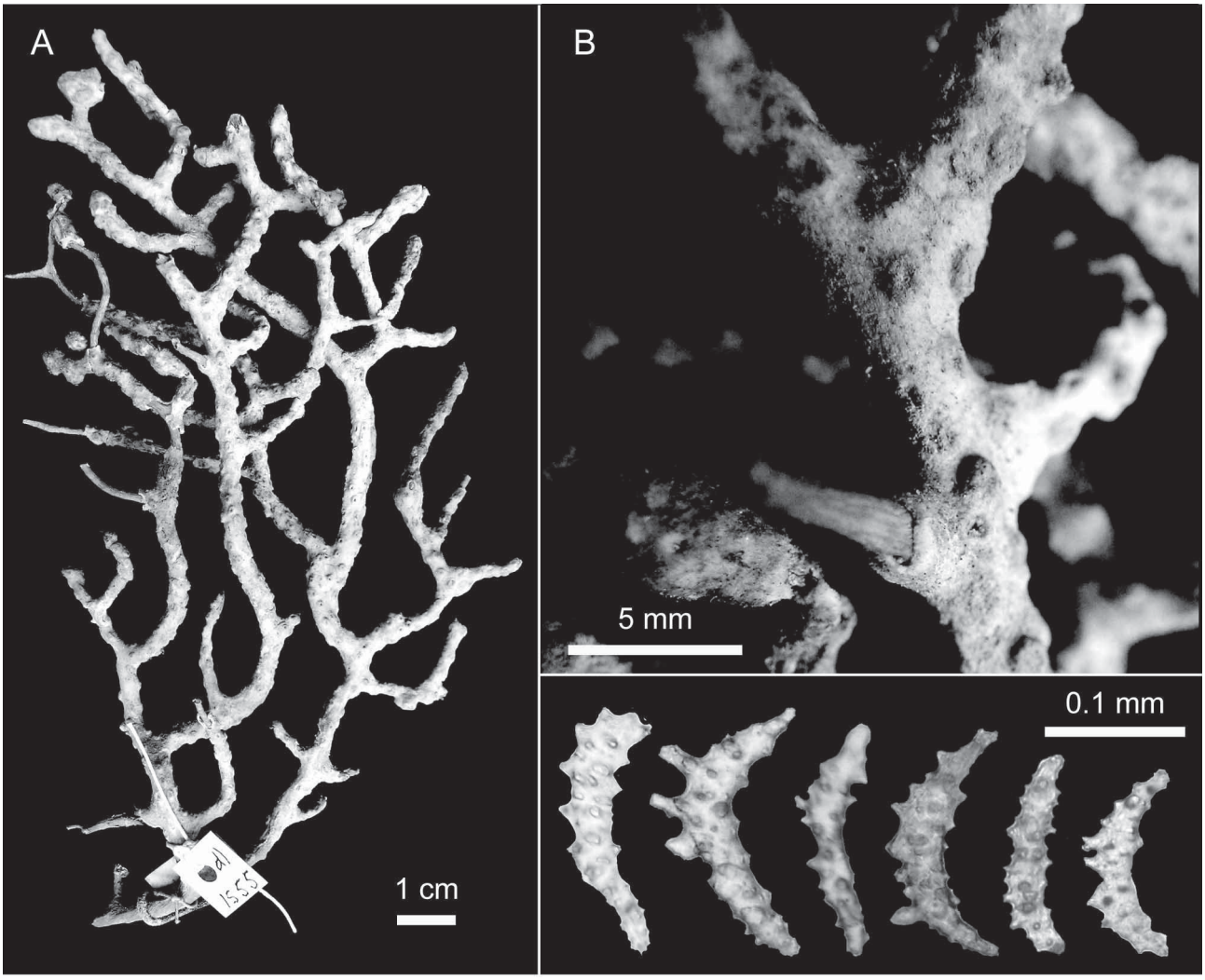

FIGURE 6. *Heterogorgia tortuosa*, lectotype, YPM 1555d: (A) colony; (B) detail of a branch; (C) tentacular sclerites.

Description of the lectotype. The colony is 13.5 cm tall and 8 cm wide (Fig. 6A–B) with a short stem that branches irregularly up to seven times. The branch diameter is 3–4 mm, and some are lacking coenenchyme, exposing the dark axis. Only a very small portion of the holdfast is preserved. The polyps retract into prominent calyces up to 1 mm tall and up to 1.5 mm diameter (Fig. 6B), and are sparsely distributed around the branches, about 1.5 mm apart, and even more distant at the base of the branches and on the holdfasts, up to 4 mm apart (Fig. 6A). Anthocodial armature consists of collaret and points. The collaret is composed of two whorls of long curved spindles, 0.27–0.55 mm long and 0.03–0.08 mm wide, which are covered with small spines (Fig. 7A); the points are composed of 2–3 pairs of spiny spindles arranged *en chevron;* they are 0.16–0.34 mm in long and 0.02–0.05 mm wide (Fig. 7B). The tentacles bear thorny rods, and crescents 0.09–0.2 mm long and 0.03–0.04 mm wide, that are ornamented on their convex side with tubercles and thorn-like processes (Fig. 6C). The calicular rim has two whorls of thick warty thorns that are 0.18–0.30 mm long and 0.04–0.05 mm wide (Fig. 7C). Coenenchymal sclerites comprise: small tuberculate radiates, 0.07–0.12 mm long and 0.06–0.09 mm wide (Fig. 7F); crosses, 0.09–0.2 diameter (Fig. 7E), with tuberculate arms; and spindles 0.12–0.4 mm long and 0.045–0.13 mm wide (Fig. 7D), that can be branched, straight or bent, and have the tips acute or irregularly tuberculate.

Colour of the colony is whitish.

Variability. The other specimens examined reach up to 14 cm tall, and 10 cm wide. The stems are connected by a continuous encrusting holdfast and subdivide close to the base into several slightly flattened branches, up to 6 mm diameter, that re-branch often in an irregular manner. When alive, the polyps are bright yellow, and the coenenchyme looks reddish or brownish (Fig. 1C). Some variation in the size of sclerites has been found in some specimens. All other characteristics are as described for the lectotype.

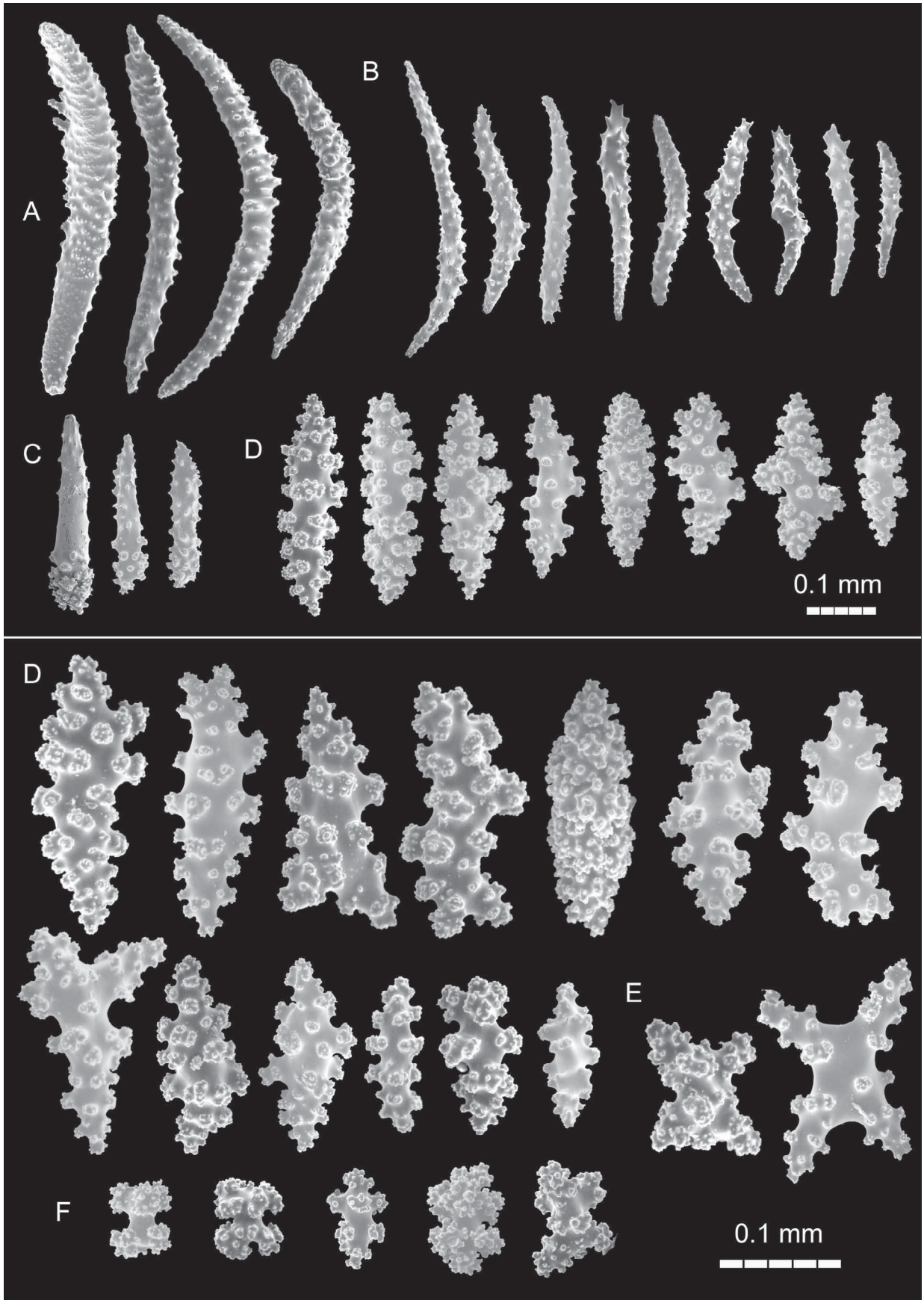

FIGURE 7. *Heterogorgia tortuosa*, lectotype, YPM 1555d, sclerites: (A) collaret spindles; (B) point spindles; (C) thorns; (D) spindles; (E) crosses; (F) radiates.

The colour of the colonies is whitish to beige or brownish in ethanol or dry preserved.

Remarks. The type series of *H. tortuosa* consists mostly of colonies in bad condition and specimen YPM 1555d was selected as the lectotype to establish the species' identity because of its better state of preservation.

This species is reported only for Costa Rica and Panama.

A comparison of this species with others is included in the Remarks section for *H. verrucosa*.

Heterogorgia uatumani Castro, 1990

(Figs. 8, 9)

Heterogorgia uatumani Castro, 1990: 415–418; Castro *et al.* 2010: 776–779; Breedy & Guzman 2005: 805.

Material examined. Holotype. MNRJ 01233, ethanol preserved, off Ponta Grossa do Sítio Forte, Grande Island, Angra dos Reis, RJ, Brazil (26°06.8′ S, 44°17.6′ W), 8–15 m, C.B. Castro and C.A. Secchin, 21 November 1982. Paratypes. USNM 73432, ethanol preserved, Grande Island, Brazil, 8–15 m, C.B. Castro, 21 November 1982; USNM 73431, two colonies, ethanol preserved, Amendoim Island, Brazil, 9–13 m, C.B. Castro, 6 November 1981; USNM 73569, three colonies, ethanol preserved, Laje dos Moleques Sao Senastiao Channel, Brazil, 6 m, P.S. Young, 4 May 1984.

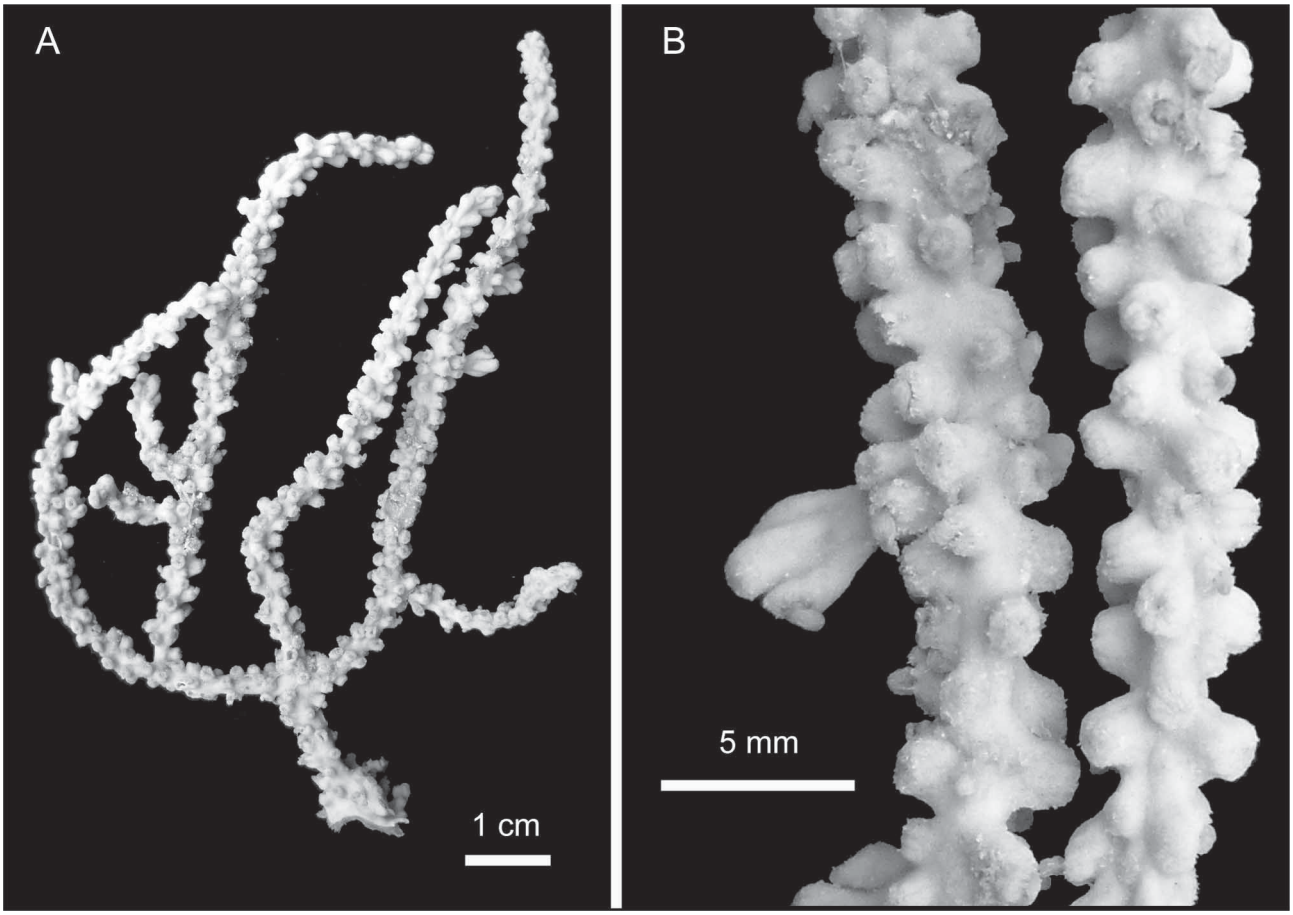

FIGURE 8. *Heterogorgia uatumani*, holotype, MNRJ 01233: (A) colony; (B) detail of a branch.

Description of the holotype. The colony is irregularly branched, up to 11 cm tall. Several stems arise from a common encrusting holdfast and branch several times mostly in a single plane, the diameter of the stems including calyces, reaches up to 4.5–5 mm, and is about the same diameter at the tip. The polyps are bright yellow when alive (Castro 1990) and distributed all around the branches, not very close together (about 12–20 calyces/cm) and more scarcely distributed on the holdfast and at the base of the branches (Fig. 8). The calyces are prominent, up to 1.5 mm tall and 1.2 mm diameter, with a weak arrangement of thorns on the rim. The anthocodial armature is com-

posed of a strong points of 5 to 6 pairs of spindles arranged *en chevron*, measuring 0.20–0.33 mm long and 0.02–0.05 mm wide (Fig. 9G), but a collaret is absent. The point sclerites are bent or straight, some with a spiny distal end, and there are sparse spines on the surface. The calicular rim bears one whorl of projecting thorns, 0.25–0.32 mm long and 0.05–0.06 mm wide and the shaft of the thorns tends to be serrated or spiny (Fig. 9G). The coenenchymal sclerites comprise: small tuberculate radiates, 0.075–0.085 mm long and 0.05–0.06 mm wide (Fig. 9E); warty ovals, 0.09–0.13 mm long and 0.06–0.10 mm wide (Fig. 9D); crosses, 0.12–0.20 mm diameter (Fig. 9C) and various types of spindles, straight, reaching 0.22–0.32 mm long and 0.07–0.1 mm wide, with acute ends (Fig. 9A), and irregularly branched or lobed, 0.18–0.30 mm long and 0.06–0.13 mm wide (Fig. 9B). The tentacles bear tuberculate rods, 0.11–0.13 mm long and 0.014–0.03 mm wide (Fig. 9H). A complete description of the holotype is given by Castro (1990: 415–420).

The colour is whitish to beige or brownish either in ethanol or dry preserved.

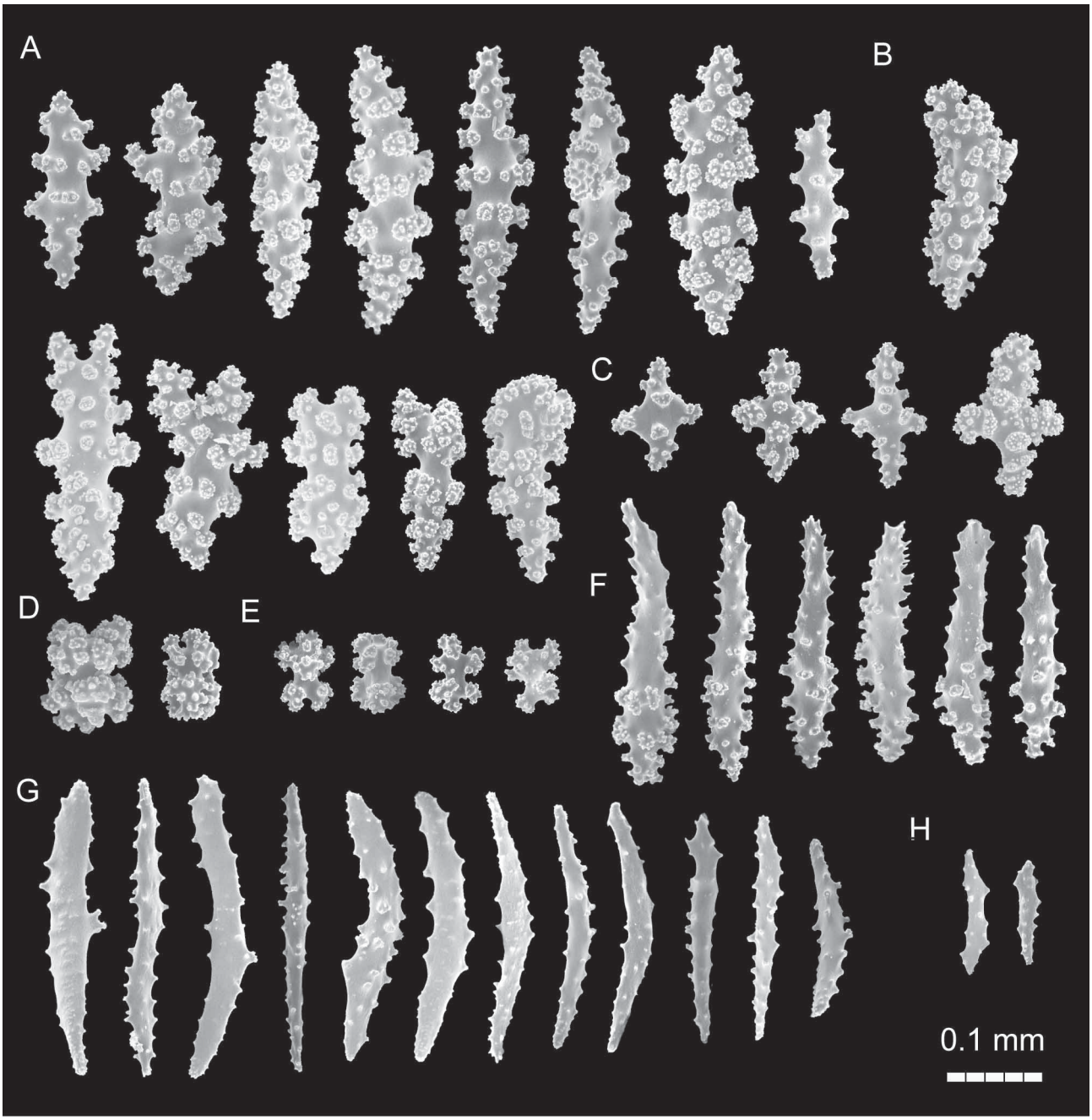

FIGURE 9. *Heterogorgia uatumani*, holotype, MNRJ 01233, sclerites: (A) spindles; (B) irregularly branched or lobed spindles; (C) crosses; (D) warty ovals; (E) radiates; (F) thorns; (G) point spindles; (H) tentacular rods.

Remarks. There is a lot of variation in sclerite shape among specimens of *H. uatumani* and even among calyces of the same specimen, especially the "palisade" sclerites (thorns around the calicular rim) (Castro, pers. com.). The absence of a collaret in this species is not consistent with this genus, and, along with other differences given in Table 2, definitely separates this species from the others. However, another more precise taxonomic allocation for this species in another genus cannot be presently resolved.

Heterogorgia uatumani is the only record for this genus in the Atlantic Ocean so far. It has been reported at various localities off the coast of Brazil, from Amapá State to Santa Catarina State (Castro *et al.* 2010), and also from the north-west Caribbean (Humann 1994), with a depth range of 6–15 m.

TABLE 2. Comparative characteristics of the *Heterogorgia* species. Diameter of branches and calyces represent the average maximum size found for each species. Sclerite ranges represent the average minimum and the maximum size measured in all the samples. All measures are given in mm.

Species	*H. hickmani*	*H. papillosa*	*H. tortuosa*	*H. verrucosa*	*H. uatumani*
Max. No. branching	2	4	7	4	4
Stem diameter	12–19	4–4.5	4–6	7–12	4–4.5
Calyces/cm	40–50	25	14	20–24	12–20
Calyx diameter	2.1	0.5	1.6	1.8	1.2
Calyx height	1	1	1	1.2	1.5
Collaret spindles	0.5–0.7 x 0.05–0.13	0.26–0.43 x 0.03–0.05	0.27–0.55 x 0.03–0.08	0.35–0.56 x 0.05–0.10	absent
Points spindles	0.4–0.5 x 0.04–0.06	0.20–0.35 x 0.02–0.04	0.16–0.34 x 0.02–0.05	0.025–0.51 x 0.04–0.05	0.20–0.41 x 0.02–0.05
Tentacular rods	0.08–0.2 x 0.02–0.05	0.10–0.16 x 0.015–0.02	0.02–0.09 x 0.03–0.04	0.10–0.24 x 0.025–0.08	0.11–0.14 x 0.014–0.03
Thorns	0.3–0.50 x 0.06–0.11	0.24–0.30 x 0.04–0.06	0.18–0.30 x 0.04–0.05	0.23–0.46 x 0.05–0.08	0.25–0.35 x 0.05–0.064
Spindles	0.25–0.45 x 0.10–0.15	0.15–0.40 x 0.04–0.1	0.12–0.4 x 0.04–0.13	0.15–0.45 x 0.05–0.2	0.18–0.32 x 0.064–0.12
Crosses	0.14–0.45	0.08–0.14	0.09–0.2	0.06–0.075 x 0.5–0.07	0.12–0.2
Radiates	0.06–0.12 x 0.04–0.07	0.07–0.09 x 0.05–0.055	0.07–0.12 x 0.06–0.09	0.8–0.10 x 0.05–0.06	0.075–0.13 x 0.05–0.12

Heterogorgia verrucosa Verrill, 1868

(Figs. 1D, 10–11)

Heterogorgia verrucosa Verrill, 1868: 414; Verrill 1869: 451–452; Nutting 1910: 89; Kükenthal 1924: 232; Prahl *et al.* 1986: 27–29.
Heterogorgia tortuosa Castro 1990: 412–415.

Material examined. Lectotype (here designated): YPM 1554a , MCZ 730 (fragment of YPM 1554a), dry, Pearl Islands, Gulf of Panama, depth not given, F. H. Bradley, 1866–1867.

Paralectotypes: YPM 1554b, MZC 36014 (two slides of YPM 1554b), dry, Pearl Islands, Gulf of Panama, depth not given, F. H. Bradley, 1866–1867; YPM 1644 a–b, ethanol preserved, Pearl Islands, Gulf of Panama, depth not given, F. H. Bradley, 1866–1867.

Other material. COSTA RICA: UCR 1715 (5), 1713 (8), preserved in ethanol, Diablillo, Caño Island, 27–30 m, O. Breedy and H. Guzman, 30 January 2007; UCR 1716 (2), preserved in ethanol, Caño Island, 30 m, O. Breedy, 1 January 2007; UCR 1848, preserved in ethanol, Bajo Hector, Caño Island, 33 m, H. Guzman and O. Breedy, 3 August 2007; UCR 1857, 1868 (4), preserved in ethanol, Bajo Mixta, Golfo Dulce, 15 m H. Guzman and O. Breedy, 7 January 2009; UCR 1860, Bajo Diablo, Caño Island, 24 m, O. Breedy, 18 February 2000; UCR 1861,

Paraíso, Caño Island, 25 m, O. Breedy, 18 February 2000; UCR 1866, Nicaragua Rocks, Golfo Dulce, 10 m, O. Breedy, 2 August 2004; UCR 1880, preserved in ethanol, Tolinga islet, Nicoya Gulf, 18–20 m, J. Cortés and O. Breedy, 22 November 2002; UCR 1882, preserved in ethanol, Velas Cape, Baulas Marine National Park, 17 m, J. Cortés, 5 October 2006; UCR 1883, Ballena 50 H003, preserved in ethanol, Ballena Rock, Ballena Marine National Park, 18 m, O. Breedy, 28 April 2003; UCR 1884, dry, Cabeza de Mono, Culebra Bay, 20 m, O. Breedy, 1999; UCR 2091, MA80B, preserved in ethanol, Olucuita islet, Manuel Antonio National Park, 20 m, O. Breedy, 5 April 2005. ECUADOR: IIN 2, dry, Tambip, Reserva de Producción Faunística Marino Costera Puntilla de Santa Elena, 12–14 m, F. Rivera, P. Martínez, R. Nebot and O. Breedy, 20 July 2010; IIN 37, dry, Gigima, Reserva de Producción Faunística Marino Costera Puntilla de Santa Elena, 12–14 m, F. Rivera, P. Martínez, R. Nebot and O. Breedy, 22 July 2010; IIN 102, dry, Los Ahorcados Islet, Provincia de Manabí, 10–12 m, F. Rivera, P. Martínez, R. Nebot and O. Breedy, 25 July 2010; GALÁPAGOS ISLANDS: CDRS Ang 8, ethanol preserved, Española, 12 m, A. Chiriboga, 23 April 2003. PANAMA: UCR 1552, UCR 1850, UCR 1857, preserved in ethanol, Jicarita, 20–22 m H. Guzman, 19 April 2007; UCR 1851, preserved in ethanol, Jicarita, 20–22 m H. Guzman, 19 April 2002; UCR 1852(2), preserved in ethanol, Frailes sur, 20–25 m H. Guzman, 12 December 2001; UCR 1867, preserved in ethanol, Jicarita, 25 m H. Guzman, 19 April 2002; STRI 253, dry; Passage Island, Chiriquí Gulf, 15 m, H. Guzman, 20 April 2002; STRI 323, dry, Frijol Islet, 5–15, H. Guzman, 24 April 2002; STRI 304, dry, Bajo Viuda, 30 m, H. Guzman, 23 April 2002 .

Description of the lectotype. It is a small, 4.5 cm tall, deteriorated colony (Fig. 10C) and a separate branch, 5 cm long (Fig. 10A), that was part of the original specimen YPM1554a. The colony is composed of three broken stems, up to 5.3 mm in diameter that are kept together by the remains of the spreading holdfast, which is 3 cm in diameter. The branches bifurcate several times in a lateral irregular manner. Calyces are up to 1.2 mm tall and 1.4–1.6 mm diameter and they are evenly distributed around the two branches that still have calyces; 22–25 calyces/cm. On the branches, the calyces are about 0.5 mm apart, but they are more sparsely distributed on the holdfast and at the base of the branches where they are about 2 mm apart (Fig. 10A). The anthocodial armature consists of strong collaret and points. The collaret is composed of 4 rows of long curved spindles, 0.35–0.56 mm long and 0.05–0.1 mm wide, that are covered with small spines (Fig. 11A). The points are composed of 3–4 pairs of spiny spindles arranged *en chevron* (Fig. 11B). They are 0.27–0.51 mm long and 0.045–0.05 mm wide, and several of them have a bifurcated end. The calicular rim has two whorls of projecting thorns, 0.23–0.46 mm long and 0.056–0.08 mm wide, measured at the proximal end, that have rather blunt tips (Fig. 11C). Coenenchymal sclerites comprise small tuberculate radiates and irregular warty ovals (Fig. 11E), 0.08–0.11 mm long and 0.05–0.06 mm wide; crosses 0.058–0.07 mm, with tuberculate arms or tuberculate all over; and spindles (Fig. 11D) 0.15–0.43 mm long and 0.06–0.18 mm wide, which are variable in shape and can be branched, which have axes straight or bent, and ends acute or irregularly tuberculate. Tentacles bear thorny rods and crescents 0.14–0.24 mm long, and 0.03–0.08 mm wide (Fig. 11F).

The colour of the colony is ivory.

Variability. The paralectotypes are up to 7 cm tall and about the same wide, and all are very consistent with the lectotype. Some variation in the diameter of the branches has been observed, but the shape of the calyces and their distribution is consistent in all colonies.

The other material examined consists of colonies that are up to 12 cm tall and 15 cm wide, composed of three to four stems (4–5 mm diameter) that arise from a common encrusting holdfast and bifurcate about 1–3.5 cm above the base. The branching is lateral and irregular; the branches sprout at different angles and ascend parallel to the main stem, some are bent at the ends (Fig. 10B). The coenenchyme is thin and firm with a granulose appearance. The polyps are retractile into calyces up to 1.2 mm tall and 1.8 mm diameter and are evenly distributed around the branches, 25–30 calyces/cm and 0.5 mm apart, but more scarcely distributed on the holdfast and at the base of the branches where they are about 2 mm apart (Fig. 10B, D). The sclerites are consistent in shape and size within the type series and the rest of collection.

The colour of the colonies is whitish to beige or brownish in ethanol or dry preserved, and when alive, the coenenchyme looks reddish and the polyps are bright yellow (Fig. 1D).

Remarks. Castro (1990) synonymised *H. tortuosa* with *H. verrucosa* based on a syntype of the *H. tortuosa* YPM 1555 series. Later, Breedy & Guzman (2005) listed differences between these two species after examining the complete syntype series of *H. tortuosa* (YPM 1555a–d). We examined a large collection of specimens in this group and found sufficient character differences (Table 2) to allow us to retain *H. tortuosa* as it was proposed by

Verrill (1868). Compared to *H. verrucosa, H. tortuosa* has a more irregular branching pattern, branches are more flattened and shorter and the calyces are more distantly placed and more acute. Also, the coenenchyme of *H. verrucosa* is more granular in appearance than in *H. tortuosa* due to more warty sclerites and/or their arrangement. Collaret and points in both species are composed of sclerites with similar sizes, but they are more sculpted, thorny and warty in *H. verrucosa*. Moreover, collaret and point sclerites are also differently arranged; in *H. verrucosa* there are 4 rows and 3–4 pairs respectively, and in *H. tortuosa* 2–3 rows and 2–3 pairs (Table 2).

The type series mostly consists of colonies in bad condition, and specimen YPM 1554a was selected as the lectotype of *H. verrucosa* to establish the species identity.

In addition to Costa Rica, and Panama, we recently found this species at the Galapagos Islands, Ecuador, Prahl *et al.* (1986) reported this species from Gorgona Island and Málaga Bay, Colombia.

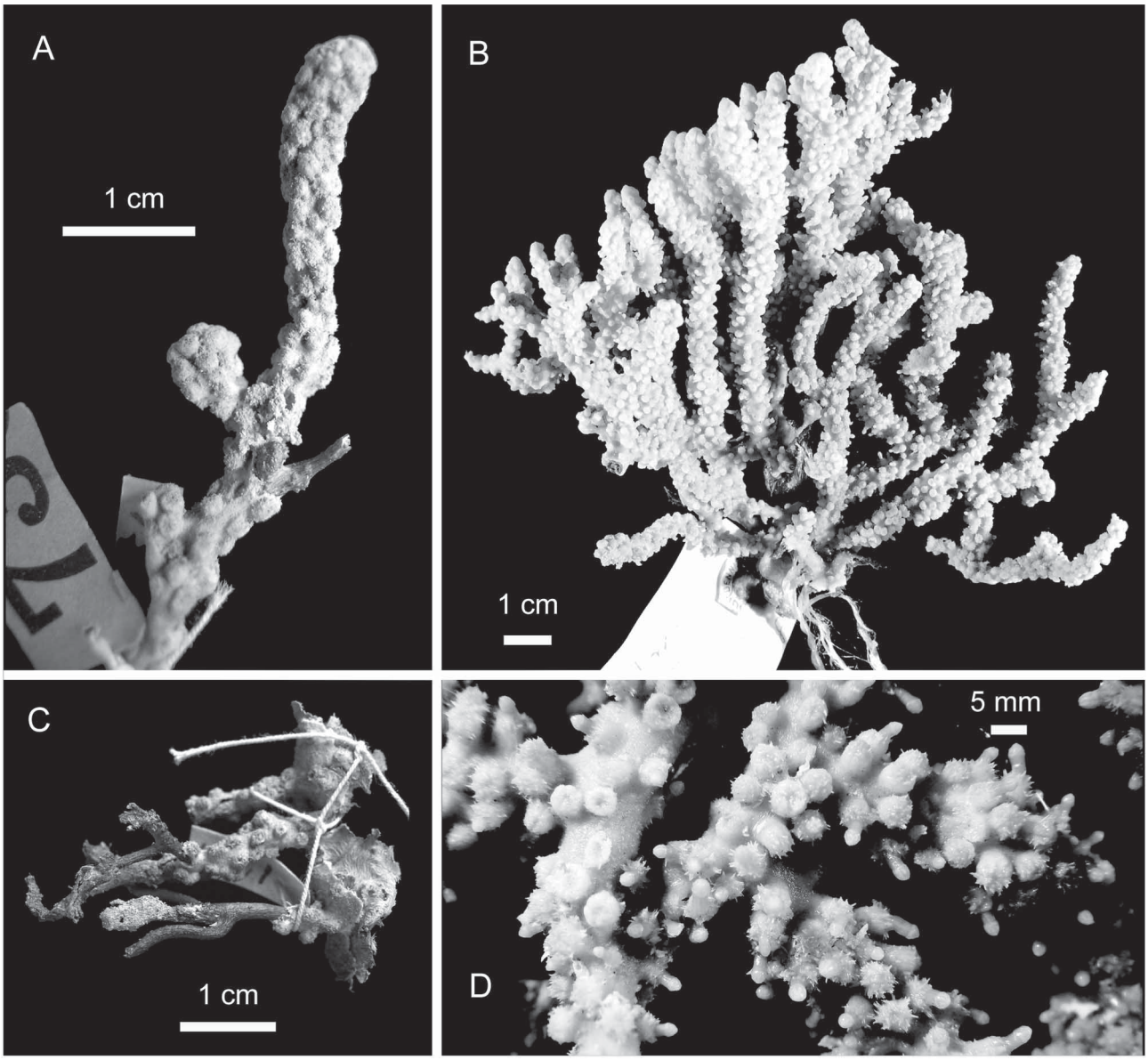

FIGURE 10. *Heterogorgia verrucosa*: (A) fragment of the lectotype, MCZ 730; (B) UCR 1715, colony ; (C) lectotype colony, YPM 1554a; (D) UCR 1715, detail of a branch.

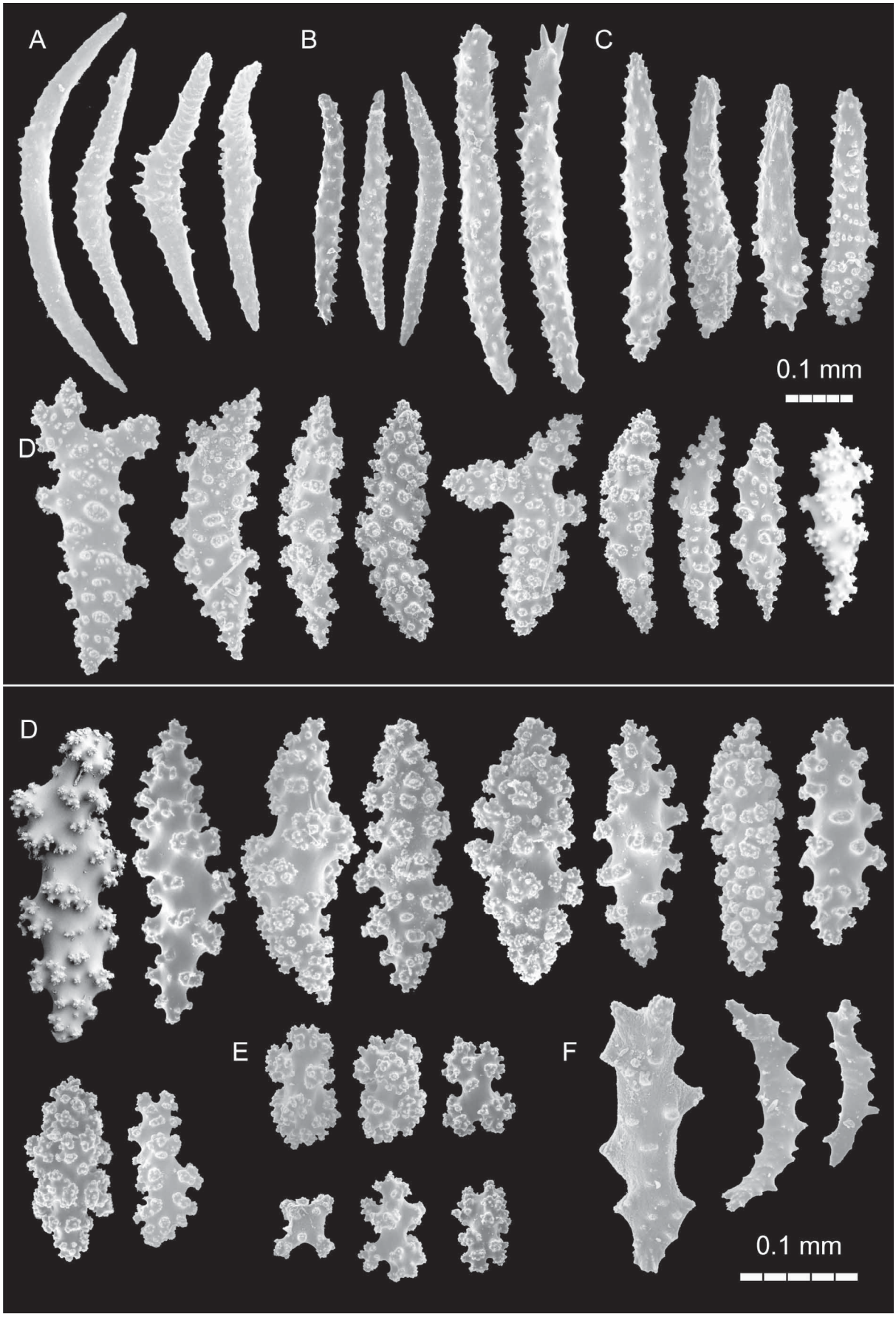

FIGURE 11. *Heterogorgia verrucosa*, lectotype, YPM 1554a , sclerites: (A) collaret spindles; (B) point spindles; (C) thorns; (D) spindles; (E) radiates and irregular warty ovals; (F) tentacular rods.

Final remarks

The genus *Heterogorgia* is comprised of a few species that live in clusters on rocky vertical walls and under ledges, or in crevices on hard bottoms. The genus has been found in shallow waters less than 40 meters in depth; one species is known, at present, only from the type locality, *H. papillosa*.

Despite some similarity in external morphology in some of the 14 species formerly assigned to *Heterogorgia*, differences, especially in the sclerites, definitely segregate them from this genus.

Based on the study of morphological characteristics (Table 2), we consider that the genus *Heterogorgia* is comprised of five valid species at present. On current evidence, *Heterogorgia hickmani* and *H. verrucosa* are restricted to the Galapagos Islands and off the Ecuador mainland; *H. papillosa* to Mexico; *H. tortuosa* and *H. verrucosa* to Costa Rica and Panama; and *H. uatumani* to south eastern Brazil, and Bahamas. It is recommended that surveys to Peru and Chile, as well as the northern coast of Brazil and the Caribbean, be increased to better assess the geographic range of the genus. In addition, regional biodiversity estimates and biogeography analyses have to carefully consider the erroneous status of the species that are still listed as *Heterogorgia* within the data sets.

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References

Bayer, F.M. (1951) A revision of the nomenclature of the Gorgoniidae (Coelenterata: Octocorallia) with an illustrated key to the genera. *Journal of the Washington Academy of Sciences*, 41, 91–102.

Bayer, F.M. (1956) Octocorallia: *In:* Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology. Part F. Coelenterata*. Geological Society of America and University of Kansas Press, pp. F163–F231.

Bayer, F.M. (1961) *The shallow water Octocorallia of the West Indian Region. A manual for marine biologists*. Martinus Nijhoff, The Hague, 400 pp.

Bayer, F.M. (1981) Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa. *Proceedings of the Biological Society of Washington,* 94, 902–947.

Bayer, F.M. (1994) A new species of the gorgonacean genus *Bebryce* (Coelenterata: Octocorallia) from Papua-New Guinea. *Bulletin of Marine Science*, 54, 546–553.

Bayer, F.M. & Macintyre, I.G. (2001) The mineral component of the axis and holdfast of some gorgonacean octocorals (Coelenterata: Anthozoa), with special reference to the family Gorgoniidae. *Proceedings of the Biological Society of Washington*, 114, 309-345.

Bayer, F.M., Grasshoff, M. & Verseveldt, J. (1983) *Illustrated trilingual glossary of morphological terms applied to Octocorallia*,

E.J. Brill, Leiden, 74 pp.
Breedy, O. & Guzman, H.M. (2002) A Revision of the genus *Pacifigorgia* (Coelenterata: Octocorallia: Gorgoniidae). *Proceedings of the Biological Society of Washington,* 115, 787-844.
Breedy, O. & Guzman, H.M. (2005) A new species of alcyonacean octocoral from the Galapagos Archipelago. *Journal of the Marine Biology Association of the United Kingdom*, 85, 801-807.
Breedy, O. & Guzman, H.M. (2007) A revision of the genus *Leptogorgia* Milne Edwards & Haime, 1857 (Coelenterata: Octocorallia: Gorgoniidae) in the eastern Pacific. *Zootaxa*, 1419, 1–90.
Breedy, O., Guzman, H.M., Vargas, S. (2009) A revision of the genus *Eugorgia* Verrill, 1868 (Coelenterata: Octocorallia: Gorgoniidae). *Zootaxa*, 2151, 1–46.
Castro, C.B. (1990) A new species of *Heterogorgia* Verrill, 1868 (Coelenterata, Octocorallia) from Brazil with comments on the type species of the genus. *Bulletin of Marine Science*, 47, 411–420.
Castro, C.B., Medeiros, M.S., Loiola, L.L. (2010) Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. Journal of Natural History, 44, 763–827.
Ehrenberg, C.G. (1834) Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systemat ik derselben. *Abhandlungen Königlichen Akademie der Wissenschaften zu Berlin.* Aus dem Jahre 1832. Erster Theil, 225–380.
Germanos, N.K. (1896) Gorgonaceen von Ternate. *In*: Kukenthal, W. (Ed.), *Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo, im Auftrage der Senckenbergischen naturforschenden Gesellschaft ausgefuhrt von Dr. Willy Kukenthal, Teil 2, Band 1.* Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 23, 145–187.
Gray, J.E. (1859) On the arrangement of zoophytes with pinnated tentacles. *Annals and Magazine of Natural History,* 4, 439–444.
Harden, D.G. (1979) *Intuitive and Numerical classification of east Pacific Gorgonacea (Octocorallia).* PhD thesis, Illinois State University, USA. Unpublished.
Hickson, S.J. (1928) The Gorgonacea of Panama Bay together with a description of one species from the Galapágos Islands and one of Trinidad. *Videnskavelige Meddelelser fra den naturhistoriske Forening i Kovenhavn for Aarene*, 85, 325–422.
Haeckel, E. (1866) *Generelle Morphologie der organismen*. Berlin. 1036 pp.
Humann, P. (1994) *Reef Coral Identification. Florida, Caribbean and Bahamas.* Paramount Miller Graphics. Inc. Jacksonville, 240 p.
Kükenthal, W. (1919) Gorgonaria. *Wissensschaftliche Ergebnisse der Deutschen Tiefsee–Expedition auf dem Dampfer "Valdivia"*, 1898–1899, 13, 1–946.
Kükenthal, W. (1924) Gorgonaria. *Das Tierreich*, 47. Walter de Gruyter and Co., Berlin und Leipzig, i–xxviii, 1–478 pp.
Lamouroux, J.V.F. (1812) Extrait d'un mémoire sur la classification des Polypiers coralligènes non entièrement pierreux. *Nouveau Bulletin des Sciences, par la Société Philomatique, Paris* 3, 181–188.
Milne Edwards, H. & Haime, J. (1857) *Histoire naturelle des coralliaires ou polypes proprement dits*, Vol. 1 pp. I–xxxiv+ 1–326, 8 plates, numbered A1–6, B1–2. Paris, à la Libraire Encyclopédique de Roret.
Nutting, C.C. (1910) The Gorgonacea of the Siboga Expedition III. The Muriceidae. *Siboga-Expedition Monograph,* 13b, 1–108.
Prahl, H. von, Escobar, D., & Molina, G. (1986) Octocorales (Octocorallia: Gorgoniidae y Plexauridae) de aguas someras del Pacífico Colombiano. *Revista de Biología Tropical*, 34, 13–33.
Pallas, P.S. (1766) *Elenchus zoophytorum systems generum adumbrations generaliores et specierum cognitarum succinactas descriptions cum selectis auctorum synonymis*, Hagae Comitum, 451 pp.
Thomson, J. & Crane, G. (1909) The Alcyonarians of Okhamandal. *In*: Hornell, J. (Ed.), *Marine Zoology of Okhamandal in Kattiawar*, 1, 125–135.
Thomson, J. & Henderson, W.D. (1905) Report on theAlcyonaria collected by Professor Herdman, at Ceylon, in 1902. *In: Report of the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar* . Part 3, supplementary report, 20, 269–238.
Vargas, S., Eitel, M., Breedy, O. & Schierwater, B. (2010) Molecules match morphology: mitochondrial DNA supports Bayer's *Lytreia-Bebryce-Heterogorgia* (Alcyonacea: Octocorallia) clade hypothesis. *Invertebrate Systematics*, 24, 1–9.
Verrill, A.E. (1868) Critical remarks on the halcyonoid polyps in the Museum of Yale College, with descriptions of new genera. *The American Journal of Science and Arts,* 45, 411–415.
Verrill, A.E. (1868a) Notes on Radiata in the Museum of Yale College, Number 6: Review of the corals and polyps of the West Coast of America. *Transactions of the Connecticut Academy of Arts and Sciences*, (Second Edition), 1, 377–478.
Verrill, A.E. (1869) Critical remarks on the halcyonoid polyps with description of new species in the Museum of Yale College. *The American Journal of Science and Arts, Series 2*, 48, 419–429.
Verrill, A.E. (1870) Notes on Radiata in the Museum of Yale College, Number 6: Review of the corals and polyps of the West Coast of America. *Transactions of the Connecticut Academy of Arts and Sciences*, (Second Edition), 1, 519–534.
Verrill, A.E. (1912) The Gorgonians of the Brazilian coast. *Journal of Academy of Natural Sciences of Philadelphia,* 15, 373–404.
Wright, E.P. & Studer, T. (1889) Report on the Alcyonaria collected by H.M.S. Challenger during the years 1873–1876. *Challenger Zoology*, 31, 314.